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ON

WHEAT MILDEW

(*PUCCINIA GRAMINIS*, *Pers.*)

AND ITS CONNECTION WITH

THE BARBERRY ÆCIDIUM

(*Æ. BERBERIDIS*, *Gmel.*)

BY

CHARLES B. PLOWRIGHT, M.R.C.S.,

SURGEON TO THE WEST NORFOLK AND LYNN HOSPITAL, CORRESPONDING MEMBER OF THE SOCIETA CRITTOGAMOLOGICA ITALIANA, AND OF THE SCOTTISH CRYPTOGAMIC SOCIETY, HONORARY MEMBER OF THE NORFOLK AND NORWICH NATURALISTS' SOCIETY, AND OF THE WOOLHOPE CLUB.

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ON WHEAT MILDEW.

CHAPTER I.

ON THE CONNECTION OF THE WHEAT MILDEW WITH THE BARBERRY,

HAS the Barberry really anything to do with the mildew in Wheat? This question is one of great practical importance to the agriculturist and through him to all classes of the community. It is by no means a novel one, and cannot be shelved as a new-fangled notion too crude to be worth investigation; for it is just a century ago, this present year, that the first recorded experiment bearing upon the question was performed, in the same county in which these lines are penned. Seventeen years ago the connection was proved to the satisfaction of Continental botanists, but many of us in this country and in America either denied it altogether or accepted it in a half-hearted sort of way. The magnitude of the interest at stake, as well as the great importance of the subject from a scientific point of view, demand that we should take the trouble to decide one way or the other. If the experiments upon which the assertion of this connection is based will not bear repeating, let us cast the vaunted theory to the winds and have done with it. But if, upon the other hand, these experiments prove the connection, let us accept it although it does uproot our prejudices and entails the acceptance of a great deal which at present we regard as too wonderful to be true, for Puccinia graminis is by no means the only case of the kind.

It was in the hope of being able to arrive at a definite conclusion one way or the other, that the writer in the summer of 1881 performed a series of experiments[*] by infecting a number of Wheat plants with ripe spores of the Barberry fungus, with this result, that while 76 per cent. of the infected plants took the disease, no less than 70 per cent. of similar Wheat plants, which were kept as check plants, became spontaneously affected with mildew. The natural conclusion arrived at was, that 6 per cent. was not conclusive evidence. It is obvious that mildew is a highly infectious disease, and the necessity for a less rough method of experiment is demanded if unequivocal results are to be obtained.

In the spring of this year (1882) another series of experiments was instituted, in which not only was the Barberry fungus sown upon Wheat, under circumstances which should, as far as possible, preclude the agency of accidental infection, but conversely the Wheat mildew was sown upon Barberry plants—with the result, it may be premised, of once again demonstrating that the Barberry fungus and the Wheat mildew are two states of one and the same fungus. Lest it should be thought I have jumped too eagerly to this conclusion it may here be said that when I began these experiments this year it was with a mind biased against the theory of "heterœcism" (that is, the occurrence of the same fungus in different phases of its growth on totally different plants), that the experiments now amount to more than a hundred, and that they have embraced many other species of Uredines besides the one which forms the subject of this paper. Had we given our forefathers more credit for the faculty of observation it would not have taken us a hundred years to arrive at our present position; nor will the time be wasted if we glance in detail at some of their writings on this subject.

HISTORY OF THE SUBJECT.

The mildew of Wheat has, as a blight, probably been known from remote antiquity. The Romans held a festival on April 25—the Robigalia, or Rubigalia—with the object of protecting their fields from mildew. The sacrifices offered on this occasion consisted of the entrails of a dog and a sheep, accompanied with frankincense and wine.[*] The fungoid nature of the mildew was not known until the latter half of the last century, for Tull,[†] writing in 1733, attributes it to the attacks of small insects "brought (some think) by the east wind," which feed upon the Wheat, leaving their excreta as black spots upon the straw, "as is shown by the microscope!" Felice Fontana,[‡] some thirty years later, published an account of the fungus with figures. Persoon,[§] in 1797, gave it the name it still bears (Puccinia graminis), and also figured it, as did Sowerby,[||] in 1799, under the name of Uredo frumenti.

The first mention of the subject immediately under consideration is by Marshall,[¶] who, writing in 1781, says:—

> "It has long been considered as one of the first of vulgar errors among husbandmen that the Barberry plant has a pernicious quality (or rather a mysterious power) of blighting the Wheat which grows near it.
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> "This idea, whether it be erroneous or founded on fact, is nowhere more strongly rooted than among the Norfolk farmers; one of whom mentioning, with a serious countenance, an instance of this malady, I very fashionably laughed at him. He, however, stood firm,

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[*] Plowright, *Grevillea*, vol. x., p. 33—41.

[*] Smith, *Smaller Dictionary of Greek and Roman Antiquities*, 5th edit., 1863, p. 322.

[†] Jethro Tull, *Horse Howeing Husbandry*, 3d edit., 1751, p. 151-2.

[‡] Felice Fontana, *Osservazioni sopra la Ruggine del Grano*, Lucca, 1767.

[§] Persoon, *Tentamen Dispos. Method. Fungorum*, 1797, p. 39, t. iii., f. 3.

[||] Sowerby, *English Fungi*, vol. ii., 1799, t. 140.

[¶] Marshall, *Rural Economy of Norfolk*, 2d edition, London, 1795, vol. ii., p. 19.

and persisted in his being in the right, intimating that, so far from being led from the cause to the effect, he was, in the reverse, led from the effect to the cause; for observing a stripe of blasted Wheat across his close, he traced it back to the hedge, thinking there to have found the enemy; but being disappointed, he crossed the lane into a garden on the opposite side of it, where he found a large Barberry bush in the direction in which he had looked for it. The mischief, according to his description, stretched away from this point across the field of Wheat, growing broader and fainter (like the tail of a comet) the farther it proceeded from its source. The effect was carried to a greater distance than he had ever observed it before, owing, as he believed, to an opening in the orchard behind it to the south-west, forming a gut or channel for the wind.

* * * * *

"Being desirous of ascertaining the fact, be it what it may, I have inquired further among intelligent farmers concerning the subject. They are, to a man, decided in their opinion as to the fact, which appears to have been so long established in the minds of the principal farmers, that it is now difficult to ascertain it from observation, Barberry plants having (of late years more particularly) been extirpated from farm hedges with the utmost care and assiduity; one instance, however, of mischief this year I had related to me; and another I was myself eye-witness to. Mr. William Barnard, of Bradfield, says that this year, seeing a patch of his Wheat very much blighted, he looked round for a Barberry bush, but seeing none conspicuous in the hedge, which was thick, he with some difficulty got into it, and there found the enemy. He is clearly decided as to the fact. Mr. William Gibbs, of Rowton, telling me that a patch of his Wheat was blighted in the same manner, and that he believed it to proceed from some sprigs of Barberry which remained in the neighbouring hedge (which a few years ago was weeded from it), I went to inspect the place, and true it is that near it we found three small plants of Barberry, one of which was particularly full of berries. The straw of the Wheat is black, and the grain, if it may be so called, a mere husk of bran, while the rest of the piece is of a much superior quality.

"These circumstances are undoubtedly strong evidence, but do not by any means amount to proof."

On October 16, 1782, Marshall[*] writes:—

"To endeavour to ascertain the truth of this opinion I had a small bush of the Barberry plant set in February or March last, in the middle of a large piece of Wheat.

"I neglected to make any observations upon it until a little before harvest, when a neighbour (Mr. John Baker, of Southrepps) came to tell me of the effect it had produced.

"The Wheat was then changing, and the rest of the piece (about 20 acres) had acquired a considerable degree of whiteness (white Wheat); while about the Barberry bush there appeared a long but somewhat oval-shaped stripe of a dark livid colour, obvious to a person riding on the road at a considerable distance.

"The part affected resembled the tail of a comet, the bush itself representing the nucleus, on one side of which the sensible effect reached about 12 yards, the tail pointing towards the south-west, so that probably the effect took place during a north-east wind.

"At harvest the ears near the bush stood erect, handling soft and chaffy; the grains slender, shrivelled, and light. As the distance from the bush increased the effect was less discernible, until it vanished imperceptibly.

"The rest of the piece was a tolerable crop, and the straw clean, except on a part which was lodged, where the straw nearly resembled that round the Barberry, but the grain on that part, though lodged, was much heavier than it was on this, where the crop stood erect.

"The grain of the crop, in general, was thin-bodied; nevertheless ten grains, chosen impartially out of the ordinary corn of the piece, took twenty-four of the barberried grains, chosen equally impartially, to balance them."

In 1784 Marshall repeated his experiment at Statfold in Staffordshire, with the same result. He says:[*]—"Upon the whole, although I have not from this year's experience been able to form any probable conjecture as to the cause of the injury, it nevertheless serves to fix me still more firmly in my opinion that the Barberry is injurious to Wheat."

Withering, writing in 1787 of Berberis vulgaris, says:[†]—"This shrub should never be permitted to grow in corn lands, for the ears of Wheat near it never fill, and its influence in this respect has been known to extend as far as 300 or 400 yards across a field."

In 1804 this country suffered severely from an outbreak of Wheat mildew, in consequence of which Mr. Arthur Young, the Secretary to the Board of Agriculture, issued a circular of questions, so as to obtain a consensus of opinion, from farmers, landowners, and others, interested in the subject, as to various points connected with causation of mildew. The ninth question ran thus:—"Have you made any observation on the Barberry as locally affecting Wheat?" The replies to these questions were published,[‡] and from them the following evidence bearing upon the question we are considering are selected.

Isaac King, Esq., Wycombe, Bucks, in answer to the question about the Barberry says:—"In 1795 a field of about 20 acres had two large Barberry bushes growing within 20 yards of it. These appeared to be the focus of destruction to several acres; in front, close to the hedge, the Wheat was as black as ink, and further off it was affected to a less degree . . . In short, I had 15 acres very good, and 5 of very little value. You may conclude the Barberries were destroyed."

Mr. S. Johnson,[§] Thurning, Norfolk, says:—"My observations on the Barberry have been for several years. I have seen the blast from a small stem blown on the Wheat in one direction upwards of 2 furlongs like smoke from a chimney."

Mr. W. Maxey,[‖] Knotting, Bucks, says:—"When passing a Wheat field a few years ago on the eve of harvest I noticed some streaks of a different and darker hue across a furlong of Wheat from the hedge directly opposite; at the end of each streak was a Barberry bush."

Mr. James Sheppard,[¶] Chippendale, Newmarket, says:—"I have never seen an instance of Wheat growing near a Barberry not being injured more or less."

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[*] Marshall, *loc. cit.* p. 359.

[*] Marshall, *Rural Economy of the Midland Counties*, 1790, vol. ii., p. 11.

[†] Withering, *Botanical Arrangement*, 1787, edit. ii., p. 366.

[‡] A. Young, *Annals of Agriculture*, vol. xliii., 1805, p. 457

[§] *Loc. cit.*, p. 469.

[‖] *Loc. cit.*, p. 505.

[¶] *Loc. cit.*, p. 510.

It is quite unnecessary to quote any further from Mr. Young's correspondents upon this point.

Sir Joseph Banks, in his paper on "Wheat Mildew," alluding to the subject before us, mentions the belief as being prevalent amongst farmers, but scarcely credited by botanists, and points out the resemblance the yellow fungus on Barberry has to rust, although it is larger. He says:[*]—"Is it not more than possible that the parasitic fungus of the Barberry and that of Wheat are one and the same species, and that the seed is transferred from the Barberry to the corn?"

This is precisely what Professor De Bary did sixty years afterwards, when he actually produced the Wheat mildew from the Barberry fungus. It must be remembered that, although these statements were made half a century ago, this in no way affects their veracity; but it may be well to quote a more recent instance in which the deleterious influence of the Barberry is shown. M. Gabriel Rivet,[†] writing in 1869, alluded to the fact that the Paris and Lyons Railway Company planted a Barberry hedge beside their line. The neighbouring proprietors drew up petitions, and asked the company to remove the hedge. The company made trials, by cutting a part of it down to see if it was really as hurtful as was alleged, and found the mildew so much diminished thereby that they had the whole hedge removed.

On July 17, 1882, I examined a field of Wheat at Flitcham, Norfolk, in the hedge of which were three Barberry bushes. Although they had been cut down a fortnight previously there was no difficulty in finding the place where each had been from the extent to which the corn was destroyed by mildew in a semicircle, about 10 yards in diameter, opposite each bush. The rest of the field was free from the disease. As a matter of fact the three Barberry bushes, or rather the places where they had been, were found by looking for the mildewed places in the Wheat. It was felt at the time that had any disbeliever in the heterœcism of the Wheat mildew been present he would have been, then and there, convinced by the logic of facts.

LIFE-HISTORY OF THE FUNGUS.

Since Persoon gave to the fungus which causes the Wheat mildew the name of Puccinia graminis, in the year 1797, our knowledge of its life history has progressively increased, owing to the researches of Tulasne and De Bary, who have shown, first, its connection with rust; then its mode of germination; and lastly, its heterœcismal character. The genus Puccinia is purely a parasitic one. Up to the present time some eighty species have been met with in Great Britain. A perfect Puccinia has no less than five kinds of reproductive forms, to which the following names have been applied, viz.:—Æcidium, Spermogonia, Uredo, Puccinia, and Promycelium. Since these various forms of fructification constitute a cycle it matters but little which we commence with, for if they be only taken consecutively we shall come round to the one with which we started. Perhaps it will be most convenient to begin with the Uredo.

FIRST STAGE: RUST—OR UREDO SPORES (FIG. 1).

Uredo linearis.—The well known rust of Wheat consists, as its names imply, of elongated masses of orange spores, which, during the summer months, occur abundantly upon the living leaves of various grasses and cereals. It is not confined to the leaves, for it frequently is found upon their sheaths, upon the stem, and also upon the glumes. If a speck of rust be examined through a common lens, it will be seen to consist of a mass of golden dust around which can be seen the torn edges of the epidermis. This yellow powder consists of oval spores, measuring from 25 to 35 mk. long by from 15 to 20 mk. wide. They are not uniform in shape, some being more globose than others, but they are all studded with minute protuberances, so as to present a warted appearance. They were originally formed beneath the cuticle of the plant, which, as they increased in size and number, they ruptured. When mature, these spores readily fall apart, and are scattered and carried away by the faintest breath of air. Examined more attentively, the majority will be found to possess at one end an appendage marking the point of their attachment to the leaf from which they sprang. If a young pustule of rust be examined in section, it will be found that each spore springs separately from a single transparent thread or tube, a portion of the mycelium or spawn of the fungus. This mycelium consists of an entanglement of hyaline tubes, ramifying between the cells of the plant that bears it; at certain points these accumulate together and give off a mass of branches, parallel to each other, all pointing towards the cuticle of the leaf. These branches become enlarged at their superficial extremities, where eventually each one produces a single spore. These spores are at first like the mycelium—colourless, but soon become filled with yellow endochrome; they then by their combined pressure rupture the cuticle, and constitute the Uredo abovementioned.

If a few fresh, ripe spores be placed upon a drop of water on a glass slide and kept in a damp atmosphere, they will in three or four hours germinate. This process is very interesting, and can easily be watched by any one who cares to take the trouble to do so. In from two to four hours most of the spores will have protruded two germ tubes from the middle of their length. These tubes come through two circular openings in the thick wall of the spore; in from five to six hours the germ tubes will be twice or thrice the length of the spore, and in them will be seen yellow granules from the interior of the spore. As a rule only one of these germ-tubes continues its growth, which it does so rapidly that in from twenty to twenty-four hours it has become many times the length of the spore. During this time nearly the whole of the yellow endochrome (contents of the cell) has passed from the interior of the spore, and from the abortive tube, to the extremity of the growing one. This tube has not only grown longer, but has taken a variable number of spiral twists like a corkscrew. It now, at the end farthest from the spore, gives off a number of irregular branches at a more or less rectangular direction. The lower end of the tube is now cut off by a septum from the empty spore-case.* If this germination has taken place upon the cuticle of the Wheat plant (or any other grass upon which the Uredo is parasitic), one or more of the branches gains an entrance into the interior of the leaf through the stomata. Once inside the leaf, the mycelium is in its proper soil and luxuriates, as before said, by ramifying between the cells of the host-plant, and in due course produces Uredo-spores. But the host plant does not live for ever; on the contrary, many of the grasses die down in winter, and although Uredo-spores have under favourable circumstances been known to retain their germinative power* for some time,

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[*] Banks, in *Annals of Agriculture*, vol. xliii., p. 521.

[†] Rivet, in *Bulletin de la Société Botanique*, vol. xvi., p. 331—334. *Influence de plantations d'epine-vinette sur la developpement de la rouille des céréale.*

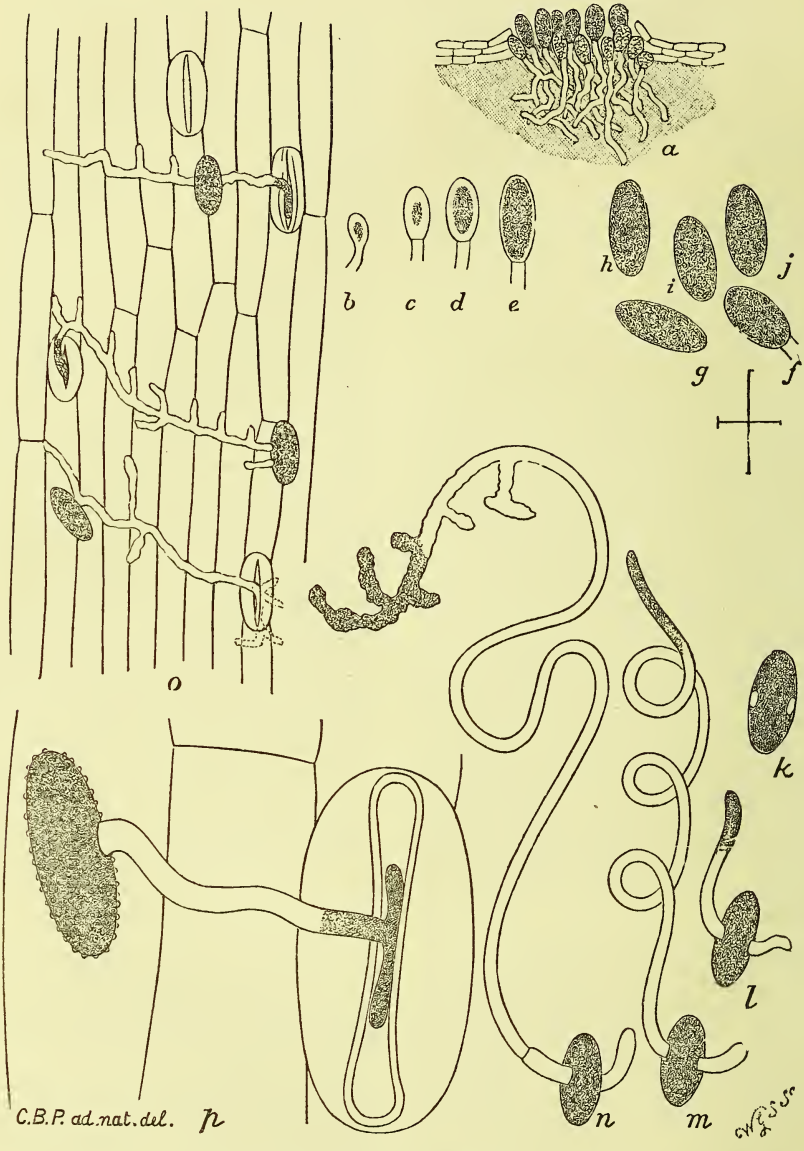

FIG. 1.—UREDO LINEARIS.

a, cluster of Uredo-spores springing from mycelium in a Wheat-plant surrounded by the ruptured epidermis; *b*, *c*, *d*, *e*, *f*, *g*, *h*, *i*, Uredo-spores of various ages; *k*, Uredo-spore germinating in water, the first change; *l*, *m*, *n*, further stages of germination in water as explained in the text; *o*, Three spores of Uredo germinating upon the cuticle of Wheat, the germ-tubes of which are entering the stomata, 8—10 hrs.; *p*, Germ-tube from a Uredo-spore squeezing itself into a stomate (7 hrs.)

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* For further account of the germination of this and other Uredines, see Plowright, *Grevillea*, vol. x., p. 138, pl. 159.

* De Bary, *Neue Untersuchungen über Uredineen*, 1865, p. 24.

yet they lose it if kept dry for one or two months at most. Probably in a state of Nature they would germinate soon after they were ripe, and so become effete. How, then, is it that this rust re-appears year after year?

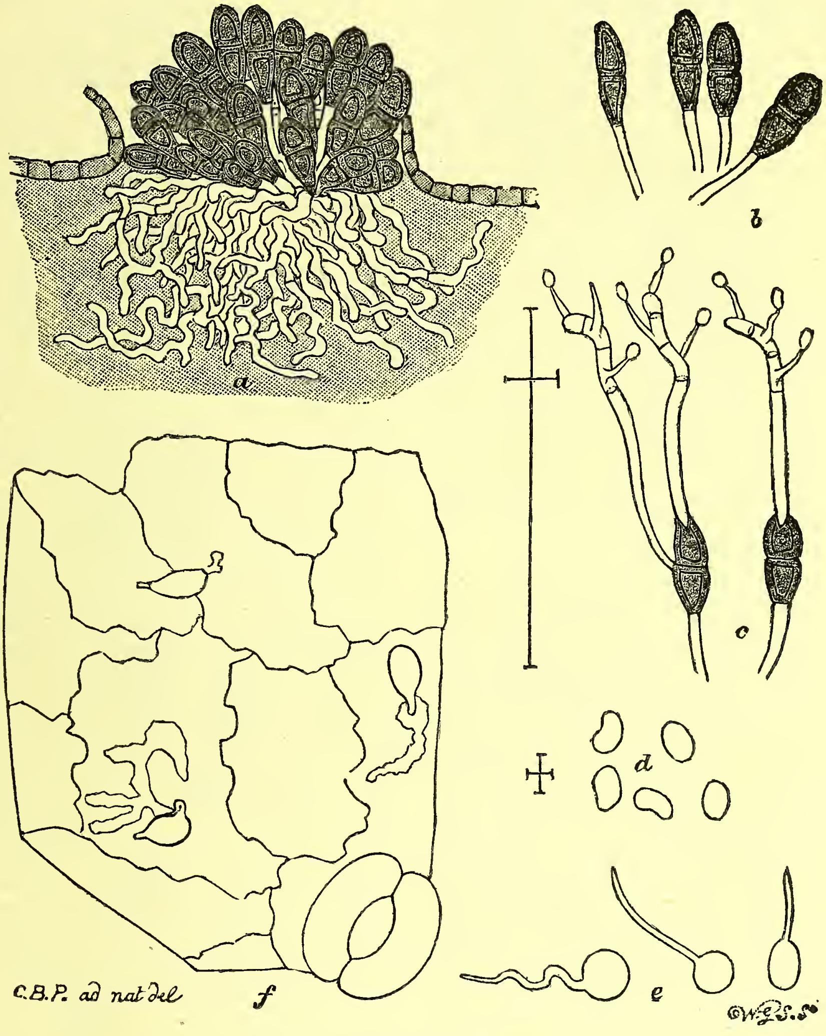

FIG. 2.—PUCCINIA GRAMINIS.

a, Mass of teleutospores springing from the mycelium and rupturing the epidermis; *b*, Four teleutospores; *c*, Germinating teleutospores bearing a promycelium and spores; *d*, Promycelium spores; *e*, Promycelium spores germinating in water; *f*, Three promycelium spores which have germinated upon the skin of a Barberry leaf. Their germ-tubes have bored their way through the epidermal cells, and have begun to form mycelium (24—48 hours).—After De Bary.

SECOND STAGE: RESTING-SPORE—PUCCINIA OR MILDEW (FIG. 2).

Towards the end of summer the mycelium, which has been continuously developing Uredo-spores, produces a resting-spore—or a body which has the faculty of lying dormant throughout the winter and germinating in spring. These resting-spores, or "teleutospores," constitute the Puccinia graminis or Wheat mildew proper. They are produced in a similar manner to the Uredo-spores, but are very different in structure. Each teleutospore is club-shaped, and divided transversely into two compartments by a septum. In colour, when seen by transmitted light, they are a rich clear brown, but appear almost black when viewed *en masse*. Inferiorly each spore has an elongated stem, by which it is permanently attached to the host-plant. They occur in elongated patches upon the straw, sometimes upon the glumes. Each patch is surrounded by the torn everted edges of the epidermis, so that mildewed straw when drawn through the fingers feels rough. The teleutospores measure from 30 to 60 mk. in length, by from 10 to mk. in breadth. Germination takes place only after a prolonged rest of some months, and consists in the protrusion of a germ-tube (the "promycelium" of De Bary), through an opening in the wall in each division of the teleutospore. These germ-tubes are of definite length, straight below, usually curved towards the extremity, often like the hook of a walking-stick. The upper part of the germ-tube gives off three simple branches which taper from base to apex; where each bears a single oval, or subreniform hyaline spore from 8 to 12 mk. by 5 to 8 mk. The end of the germ-tube is divided into three parts by septa, from each of these divisions a tapering spore-bearing branch arises. The spores, although hyaline, are faintly tinged of a pale yellowish hue. These spores, when placed in water, after a short time again germinate by sending out a slender germ-tube. Now it is upon the life-history of these spores, or promycelium spores, as they may for distinction's sake be called, that the main question we have under consideration hinges. If they be placed upon a Barberry leaf their slender germ-tubes bore right through the epidermis of the leaf into its interior, where they produce a mycelium, which, in the course of about eight days, manifests its presence by development of the first signs of the Æcidium or Cluster-cup. This is no mere figment of imagination, but a physiological fact, that can be proved by any person so disposed.

Experiments with Promycelium Spores.

In the spring of this year (1882) Mr. James Bird, of Downham, kindly gave me six small Barberry bushes (Berberis vulgaris), about 10 inches high. On April 14, April 17, and May 9 respectively I infected one of these with spores from the promycelium of Puccinia graminis from Wheat and Twitch, and kept the remaining three Barberries as control plants. In due course the Æcidium appeared upon the infected plants, the control plants remaining free from Æcidium, and they continued so for two months, when they were cut down, the experiment being then ended. If the promycelium spores, however, are placed upon the epidermis of a living Wheat plant, contrary to what one would expect, they do not enter it. De Bary* says, "The sowing of the promycelium spores gave me, as they had previously done†, the unexpected result that the germ-tubes did not penetrate the epidermis of the mildew or teleutospore-bearing host-plant. Upon the various parts of Triticum repens, T. vulgare, and Avena sativa, they remained as if they had been sown upon a glass plate; the tubes turned irregularly in the most different directions and died off, the infected grass-plant remaining intact."

On April 15 and 17 I placed upon nine Wheat seedlings some of the same promycelium spores which were used for infecting the Barberries, and upon May 7 one of the Wheat plants had rust or Uredo upon it. As these plants were, however, exposed to the air for fourteen days, an element of doubt is admitted, although an equal number of check plants grown in the open air in the same garden remained free from rust. That they did not contract the parasite from the Barberries in my garden is clear from the fact that there were no Æcidium-spores there until many days later.

Third Stage: Cluster-cups—Æcidium (fig. 3, p. 9).

The Æcidium berberidis, which, under any circumstances, must be regarded as the result of the promycelium spores of Puccinia graminis, is a far more attractive fungus from an æsthetic point of view than either of the preceding forms, when seen by a low magnifying power; it is seen to consist of a beautiful cluster of minute cups filled with golden-yellow spores. These cups are formed of a membrane, which forms a circle of whitish teeth round their mouths. They are always in groups, and are cylindrical in form. The spores which fill them are subglobose, smooth, golden-yellow, and measure from 15 to 25 mk. in diameter. They, like the Uredo-spores, are developed from mycelium, but in quite a different manner; for, instead of being produced singly, they are formed in chains, one above another, from the bottom of the cup. The oldest and ripest spore being at the top—this when mature falls off, to be succeeded in the course of a few hours by the one next below it. If a leaf with the Æcidium upon it be put upon a glass slide, it, in the course of a few days, will deposit a mass of yellow dust. If a small quantity of this powder, which, of course, consists of spores that have been shed by the Æcidium, be placed on a drop of water, few, if any, of the spores will germinate, for the reason that they are immature and have fallen out of the cup because the plant has lost some of its moisture by evaporation. It is important to bear this in mind, as it is often the cause of failure in experimenting with the Uredines. The ripe Æcidium-spore germinates in the same manner as the Uredo-spore does. The germ-tube is protruded through one of the six openings which exist, at any rate potentially, in the epispore. The yellow endochrome is passed in the same way to the end of the convoluting branched germ-tube, which is destined to enter the stomata of a graminaceous plant. If, however, the Æcidium-spores fall—as they, of course, constantly do—upon the Barberry leaves, they do not reproduce the Æcidium berberidis, for if their germination be watched upon the cuticle, it will be found that their germ-tubes do not enter the leaves. Hence they differ very considerably from the Uredo-spores, which, it will be remembered, continuously reproduced themselves upon their host-plant. Neither will the germ-tubes of the Uredo-spores, if the latter be sown upon Barberry leaves, enter them. Nor is the Æcidium ever produced from the Uredo-spores.

Fourth Form: Spermogonia (fig. 4, p. 10).

Besides the Cluster-cups there exists in company with the Æcidium another important set of reproductive organs, which are developed from the same mycelium, and to which the name Spermogonia has been applied. Spermogonia can be seen as minute dark specks upon the opposite side of the leaf, and immediately over the place occupied by the Æcidium. In point of time they are the first organs produced by the mycelium of the promycelium spore, and they last as long as the Æcidium does. Sometimes they are

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* De Bary, *loc. cit.*, p. 24, 25.

† De Bary, *Champ. Paras.*, p. 86.

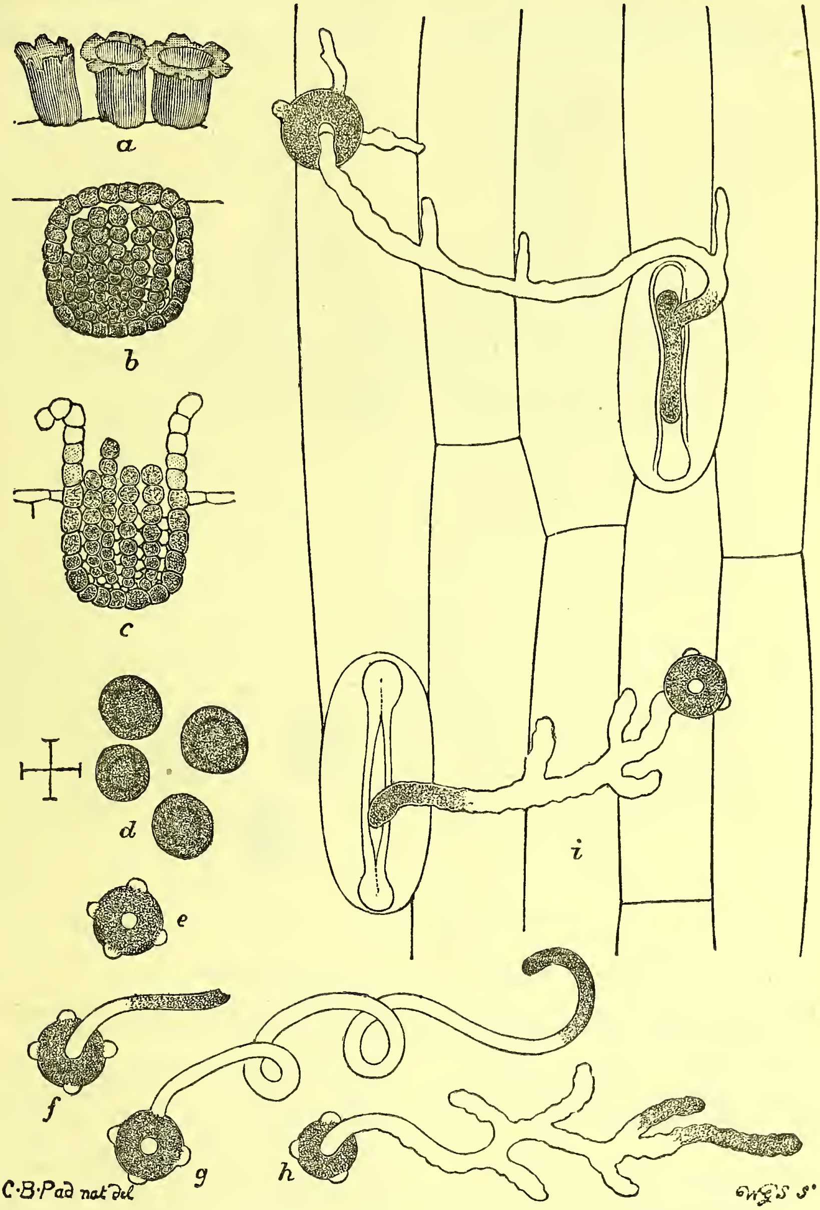

FIG. 3.—ÆCIDIUM BERBERIDIS.

a, Three cups; *b*, An immature cup before its upper wall has ruptured; *c*, Mature cup; *d*. Æcidium-spores; *e*. Æcidium-spore just beginning to germinate in water; *f*, *g*, Germination more advanced (in water); *h*, Æcidium-spore which has germinated upon the cuticle of a Wheat-plant; *i*, Cuticle of Wheat, with two spores of Æcidium upon it, the germ-tubes of which are entering the stomata. (8 hrs.)

produced alone, and are not accompanied by the Æcidium,* but this is an exceptional although not unique occurrence. Each spermogonium consists of a flask-shaped body, sunk in the substance of the leaf, formed of exceedingly delicate threads about half the diameter of those of the mycelium, and originating from them (De Bary). The mouth of the flask is conical, and by pressure is easily split from top to bottom into parallel fibres or elongated cells. The interior is filled with delicate threads which bear upon their ends chains of exceeding minute bodies, called spermatia. The spermatia vary a good deal in size and form, some are elongated, others nearly spherical; they measure from 2 to 3 mk. by .5 to 2 mk. Their function has not as yet been absolutely demonstrated, but there is little doubt that they play the part of the male element. If I am not greatly mistaken, they are the bodies one so constantly sees surrounding and adherent to the spores of many species of Æcidium.*

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* Cooke, *Microscopic Fungi*, edit. 4, 1878, p. 29.

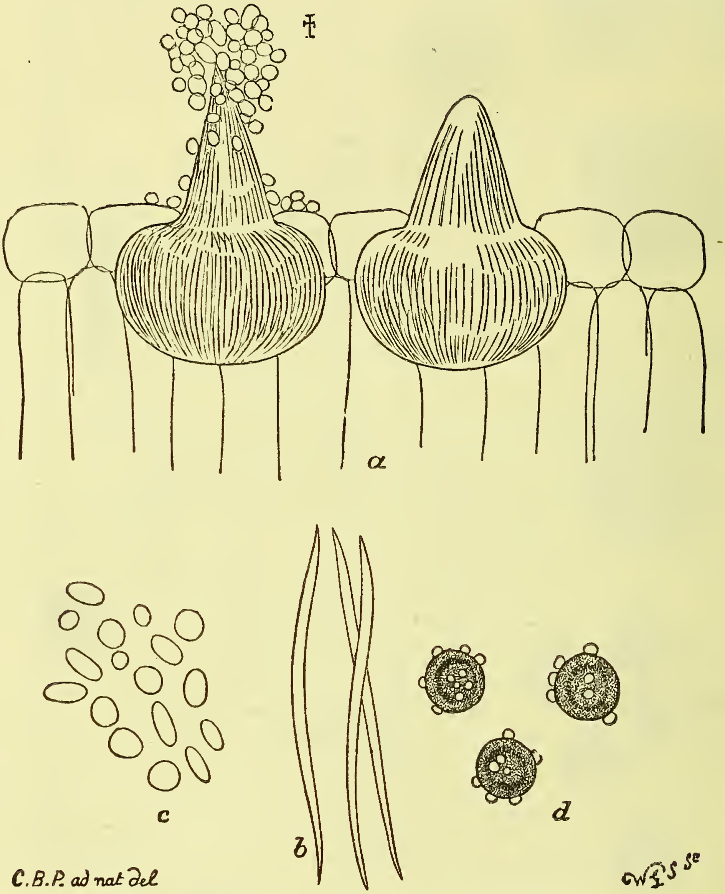

FIG. 4.—SPERMOGONIA OF ÆCIDIUM BERBERIDIS.

a, Two spermogonia upon the upper surface of a Barberry leaf; *b*, Fibres of which the mouth of the spermogonium is formed; *c*, Spermatia, very much enlarged; *d*, Two Æcidium-spores with spermatia (?) adhering to them.

The germination of ripe Æcidium-spores may be watched upon the cuticle of a Wheat plant, and the way in which their germ-tubes squeeze into the stomata easily seen.

EXPERIMENTS WITH ÆCIDIUM-SPORES.

On May 23 I infected twenty Wheat plants with ripe Æcidium-spores that had been sent me from Drayton Rectory. These Wheat plants had been carefully protected from accidental infection by being continuously covered with a bell-glass from the day they were sown until the experiment was concluded. On June 4, Uredo appeared upon ten of these plants. I then removed the plants to my study, where day by day the Uredo made its appearance upon fresh plants until the whole were affected. An equal number of Wheat plants were kept as a control experiment; they were protected in the same way from accidental infection, and remained perfectly free from Uredo the whole time.

Concerning the Barberry Æcidium it only remains to add, that there are at least two other Æcidia upon various Barberries that are in no way connected with Puccinia graminis. One of these has only been found in Chili, where Gay met with it some forty years ago. It is mentioned by Montagne* as occurring in company with a Puccinia on the leaves of Berberis glauca. De Bary† examined an original specimen of Montagne's plant, and found the spores to be twice the size of the Puccinia graminis Æcidium, and he also found the Puccinia berberidis, Mont., differed not only from P. graminis but from all other European Pucciniæ.

In 1875 Dr. P. Magnus‡ drew attention to the occurrence in various parts of Europe of an Æcidium

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[*] Plowright, in *Grevillea*, vol. x., p. 140, t. 159, f. 2.3.

[*] Montagne, *Sylloge*, p. 314, No. 1138.

[†] De Bary, *loc. cit.*, p. 31, 32

[‡] Magnus, *Hedwigia*, vol. xv., No. 1876, p. 2.

upon Barberry, which was originally described under the name of Æ. magelhanicum by Mr. Berkeley[*] from specimens collected by Captain King at Port Famine, in the Straits of Magellan, upon Berberis ilicifolia. It differs from the Æcidium of Puccinia graminis in appearing earlier in the year, in its cups being less elongated, and in their being scattered upon the under-side of the leaf, in the spores being larger, and in their germ-tubes not entering the leaves of grasses. It is probably identical with the Æ. graveolens collected by Shuttleworth at Berne in 1833, as mentioned by Dr. Cooke.[†]

The foregoing account of Puccinia graminis includes the principal facts at present known concerning its structure and life-history. That one stage of its existence is passed as a parasite upon the Barberry does not admit of doubt. But the question presents itself, Is this an absolutely essential stage, or can the mildew be propagated without the intervention of the Æcidium state? The principal reason which suggests this question is the disproportion which exists in England between the amount of mildew and the number of Barberry bushes. Especially does this obtain in Norfolk, where this shrub has been to a great extent exterminated. It is a matter of common observation that stray Wheat plants, grown upon a heap of farmyard manure, are almost invariably attacked by mildew. This has been asserted to be due to over-nitrogenous stimulation, but no amount of nitrogen has ever yet produced a Uredo or any other spore. It is worth remembering that a Wheat plant, so situate, must, during the spring, be surrounded by an atmosphere loaded with promycelium spores from the Puccinia, which is invariably formed upon straw, and it is only reasonable to suppose that these spores have a greater chance of infecting a plant than when in artificial culture a limited number is placed before the fragment of a leaf and examined under the microscope.

But assuming that De Bary is right in his view, that these promycelium-spores cannot enter the Wheat plant, is there any way in which the Uredo can be produced other than by the implantation of Æcidium-spores? It is improbable that the mycelium is perennial even when affecting perennial grasses.[‡] During the winter months in a not exceptionally severe winter it is possible to find stray pustules of Uredo either upon Wheat, or more commonly upon Twitch, growing in sheltered situations. Thus last December (1881) I found a fresh pustule of Uredo upon Twitch (T. repens) in a wood, and also one in the month of March on a hedge bank at Flitcham. This spring our Norfolk and Suffolk Wheats were much affected with rust; some of this may and probably was due to Uredo linearis, kept alive from the previous autumn, but the bulk of it was due to the Uredo of Puccinia straminis, which is always an earlier Uredo than that of P. graminis.

There is a wonderful difference in the amount of injury done by mildew when derived directly from the Barberry, and when derived from Uredo that has reproduced itself through several generations. This is very obvious from the fact, that the Uredo is to be found every year in almost every—if not in every—cornfield, but the farmer takes no notice of it, as it does not appreciably diminish the yield. But with the mildew which occurs in the middle of the Barbery bush the case is different. The fungus grows with such energy that it so injures the Wheat plant as to prevent it producing more than a few starved kernels. With such vigour does the mycelium grow and fructify at the expense of the Wheat, that the straw of the latter frequently does not ripen, but dies green. This is only what one would expect when the fact is taken into consideration, that the Æcidium spore is a sexual product, whereas the Uredo spore is not.

The practical inference clearly is, that the fewer the Barberry bushes in a district the less will that district suffer from mildew. The Æcidium of Puccinia graminis is, however, not confined to the common Barberry (Berberis vulgaris), but also occurs upon B. ilicifolia, B. canadensis, and B. nepalensis,[*] upon B. amurensis, B. aristata, and B. atro-pupurea,[†] and also upon Mahonia glauca.[‡]

I have been informed, that during the last few years the game preservers of Norfolk have been rather extensively using some varieties of Barberry as cover for game in their plantations; which variety has been employed I cannot say, but the practical importance to the agricultural community is considerable. Appended is a list of the grasses upon which Puccinia graminis is known to occur. In this country I have met with it upon Wheat, on Twitch (Triticum repens), Dactylis glomerata, Poa pratensis, Lolium perenne, and Avena elatior.

List of Grasses upon which Puccinia graminis has been known to occur:—

Phleum pratense
Alopecurus pratensis
,, fulvus
Phalaris arundinacea
Agrostis vulgaris
,, alba
Calamagrostis epigejos
Aira cæspitosa
Avena sativa
,, fatua
,, pratensis
,, flavescens
,, elatior
Poa annua
,, nemoralis
,, pratensis
Molinia cœrulea
Holcus lanatus

Dactylis glomerata
Festuca gigantea
,, spectabilis
,, tenella
Bromus mollis
,, tectorum
Triticum vulgare
,, repens
,, caninum
Secale cereale
Lolium perenne
Elymus arenarius
,, glaucifolius
Hordeum vulgare
,, sylvaticum
,, murinum
,, distichum

Charles B. Plowright, King's Lynn, July 20.

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[*] Berkeley, in Hooker's *Flora Antarctica*, vol. ii., p. 450, pl. 163, fig. 2.

[†] Cooke, *Fungi, their Nature, &c.*, p. 203, f. 108.

[‡] De Bary, *loc. cit.*, p. 23.

[*] De Bary, *Untersuchungen über Uredineen*, ii., 1866, p. 207.

[†] Winter, *Hedwigia*, vol. xix., 1880, p. 41.

[‡] Berkeley and Browne, *Annals Nat. Hist.*, Jan. 1875. It was found by my friend, Rev. J. Stevenson, at Glamis, Forfarshire; but he informs me he has not met with it since upon this plant.

CHAPTER II.

PUCCINIA RUBIGO VERA.

It has long been known that two kinds of rust affect Wheat, one of which, a state of Puccinia graminis, has been fully described in a recent number of the *Gardeners' Chronicle* in its connection with the Barberry Æcidium. The other kind of rust is less important to the agriculturist, because it seldom produces any very great amount of injury to the corn crop; yet it does do so sometimes, especially when it attacks the ears. In a recent article upon the agricultural prospects of the country in one of the daily papers, it was said that the red-rust which occurred upon the Wheat plant in March and April * "was considered to afford only a salutary check to premature development, and the Wheat plant soon recovered." It is difficult to understand how a parasitic fungus which has once gained admission into the interior of Wheat or any other plant can exert a salutary influence, especially when it is borne in mind that this rust is only the early stage of an after-coming Puccinia. Surely the Wheat plant would under any circumstance have enough to do to nourish its own fruit without having at the same time to support a parasite, which will last as long as the Wheat itself does. The red-rust at present under consideration was for a long time thought to be a fungus *sui generis*, but is now known to be only the state of a Puccinia.

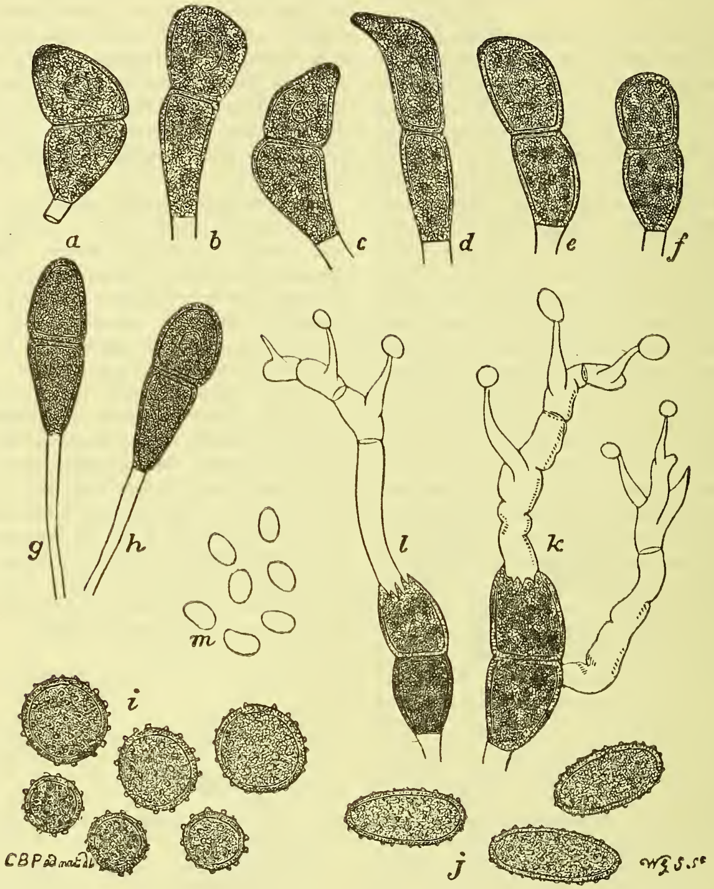

FIG. 5.—PUCCINIA RUBIGO VERA, DC.

a, b, c, d, e, f, Teleutospores of various forms; *g, h,* Teleutospores of Puccinia graminis, showing comparative size and form; *i,* Six Uredo spores of Puccinia rubigo vera; *j,* Three Uredo spores of Puccinia graminis, showing comparative size and form; *k,* Teleutospore of P. rubigo vera on Holcus, which has thrown out two promycelium tubes—May 25, 1882; *l,* ditto, in which one upper cell only has germinated: the lower cell is darker, from the endochrome still being retained in it—May 25, 1882; *m,* Promycelium spores.

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* *Daily News*, July 24, 1882.

This Puccinia has not yet been figured in this country, in fact has only been recognised as British since 1878, and I am not aware that any one has pointed it out otherwise than as a botanical curiosity, although, as has been stated above, its Uredo state has been known for many years.

Last spring, during the months of March, April, and May, many of my agricultural friends were greatly alarmed by the unusual quantity of rust upon their Wheats. To such an extent did this occur that my friend Mr. W. Marshall of Ely heard of instances of persons walking through Wheat "who had their boots and trousers covered with the red-rust." In some specimens of Wheat sent to me for examination, I found Uredo certainly upon them, but every yellow patch was not accompanied by spores. This turning yellow of the blade was ascribed by gentlemen who had been connected with agriculture from their youth to the action of frost, and doubtless the cold frosty nights we then had were the exciting cause. The mycelium of the fungus was present in the Wheat plant, and had so reduced its vitality that when the depressing influence of frost came, the chlorophyl was changed, the plant being unable to withstand the cold nights and sunny days. The sickly yellow look of the crop at this time was observable as one drove about this part of Norfolk, and from our severe visitation of mildew last year it was not surprising that those having a large interest at stake should be alarmed. Now although the frost showed us the extent to which the disease prevailed, it does not by any means follow that it did harm, on the contrary its action was beneficial. In causing the death of the affected leaves, it caused the death of the mycelium, which, although unseen, existed in them, inasmuch as the Uredines grow only in the tissues of living plants. Of course all the mycelium was not killed, but a great part of it undoubtedly was.

Puccinia rubigo vera (figs. 5, 6), like P. graminis, is a heterœcismal fungus, that is to say, it passes a part of its life history in the tissues of some other plant. It is unnecessary to go into the same details as were discussed in my previous paper upon Puccinia graminis (pp. 5—8), all that is required is to mention the points in which these two fungi differ from one another. To begin, as was then done, with the Uredo—Uredo rubigo vera, DC.[*] Uredo rubigo, Berk.,[†] Cæoma rubigo, Link,[‡] Trichobasis rubigo vera, Lév., Trichobasis glumarum, Lév.,[§] are various names which have been given from time to time to this fungus. It is smaller and more yellow, covered longer by the unruptured cuticle, with smaller and more globose spores than the Uredo of P. graminis. It germinates in a similar manner, and enters the stomata of the host-plant. One great point of difference, however, is that it appears much earlier in the year—it may be commonly met with upon Holcus lanatus in April and May, while the Uredo of Puccinia graminis is seldom found until June and July. The teleutospores (Puccinia rubigo vera, DC.) have also received more than one name, viz., P. striæformis, West.,[*] P. straminis, Fuckel.[†] They differ from those of P. graminis in being shorter, broader, more irregular, in having very short stalks, and being for a very much longer time confined under the cuticle. The individual pustules are very much smaller and less conspicuous. But perhaps the most remarkable difference is that they are not free amongst the cells of the plant but are surrounded on all sides and below by a number of dark brown bodies called paraphyses. They germinate in spring after a winter's rest and produce promycelium and spores. The germ tubes they emit are, according to my observation, shorter and wider. I was very anxious to watch the heterœcism of this fungus in spring. The Æcidium is so rare in this county that I knew it was useless to hope to obtain it. The promycelium spores were therefore the only resort, but I failed in obtaining a sufficiency for my purpose, although I applied to my friends, Dr. G. Winter of Zurich, Dr. Paul Magnus of Berlin, M. C. Roumeguére of Toulouse: it was only to hear that the season had gone by for this year. Herr E. Rostrup, however, sent me two specimens from Denmark, one on Wheat the other on Holcus, but I was not able to get them to germinate. The two teleutospores which are figured germinating were from a specimen in my herbarium collected in July, 1881, and kept dry until May, when, even under these unnatural circumstances, a few of the teleutospores did produce promycelium and spores.

Æcidium asperifolii, Pers., is the Æcidium which De Bary[‡] has proved to be produced when the promycelium spores of Puccinia rubigo vera are placed upon the cuticle of Lycopsis arvensis and Anchusa officinalis. He has figured them with their germ tubes boring through the cuticular cells of these plants,[§] and developing mycelium below [||] in the substance of the leaf. He also found that the spores of Æcidium asperifolii, sown upon young Rye plants on the 1st and 3d of August, produced the Uredo of P. rubigo vera by the 9th and 11th respectively. The spores of this Æcidium are thickly warty, polygonal, and orange-yellow. It must be a rare species, for I have searched diligently for it for some years past, and that especially this year, but always without success, although it is said to have been found near Kings Lynn several years ago. Here, therefore, we have the clearest possible indication that this heterœcismal Puccinia must have some other way of reproducing itself without the intervention of the Æcidium; how this is effected is a problem I will endeavour to solve, next year if I can, and I am not without hopes of being able to do so.

Puccinia rubigo vera is unusually abundant this year, not only upon various grasses, such as Holcus lanatus, H. mollis, Bromus sterilis, and Hordeum murinum, but also upon Rye and Wheat. Upon the former I found it not only abundant upon the leaves and stem, but also upon the glumes. Upon the latter, since Mr. Marshall sent me teleutospores a week ago, I have found it in great abundance in every Wheat field, and I have examined since then a great many in various villages around Kings Lynn. A variety of Puccinia rubigo vera, the var. simplex of Körnicke,[*] occurs in Germany and Denmark as well as in this country. It was first described by Fuckel[†] as a distinct species, under the name of P. Hordei; on the upper surface of the leaves and on the sheaths of Hordeum murinum. Specimens were published by Thümen,[*] under the name P. anomala, Rostrup.

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[*] De Candolle, *Flore Franç.*, vi., p. 83.

[†] Berkeley, *English Flora*, vol. v., part ii, p. 375.

[‡] Link, *Linn. Spec. Plant.*, vol. vi., part ii., p 4.

[§] Lévéillé, *Annales des Sciences Naturelles*, 1846–8.

[*] Westendorp, *Bullet. de l'Acad. de Belgique*, xxi., *Notice s. quelques Crypt.*, iv., No. 40.

[†] Fuckel, *Ennumer. Fungi Nassau*, p. 9, No 41.

[‡] De Bary, *Neue Untersuchungen über Uredineen*, 1866. p. 208.

[§] De Bary, *loc. cit.*, p. 215, figs. 3, 4, 5.

[||] De Bary, *loc. cit.*, p. 210.

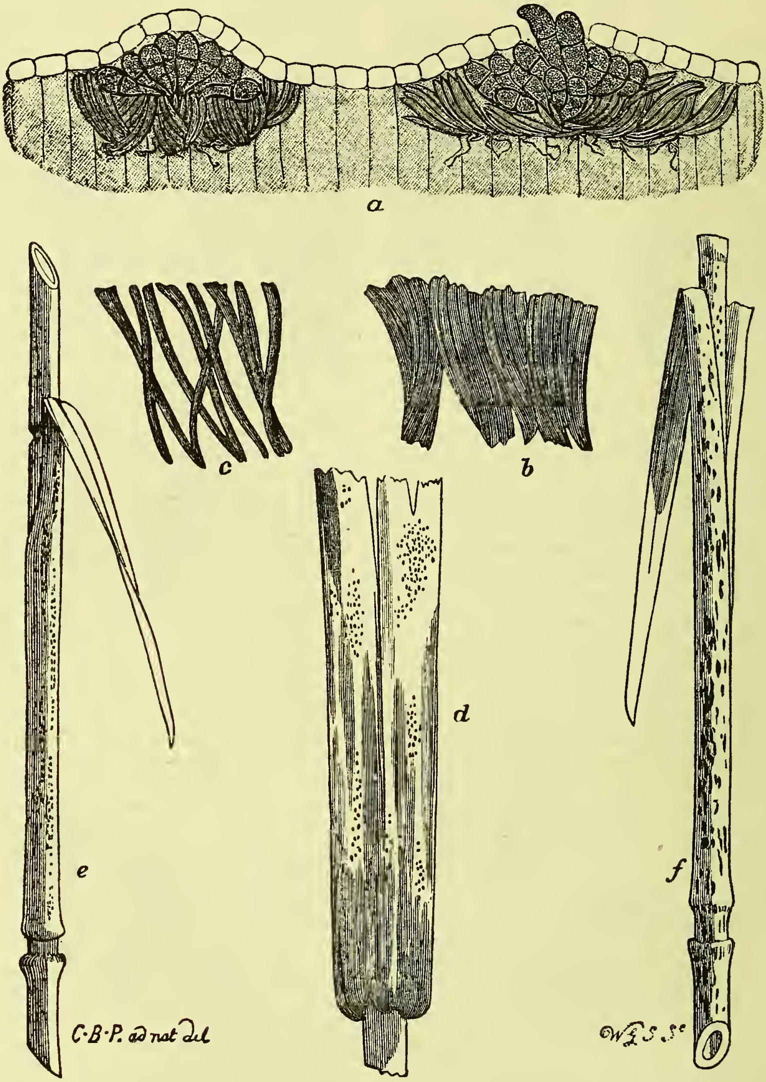

FIG. 53 —PUCCINIA RUBIGO VERA.

a, Two pustules, showing the subepidermal nature of the fungus, and bed of paraphyses; *b*, Group of paraphyses; *c*, Separate paraphyses; *d*, Part of a blade of Wheat with the Puccinia rubigo vera upon it; *e*, A piece of straw with the same; *f*, A piece of straw affected with Puccinia graminis, for comparison.

It is characterised by the small size of its pustules, and by the teleutospores being nearly or entirely one-celled, the upper compartment being more or less in abeyance. The teleutospores measure 44 mk. long by 20 mk. wide.

There is no doubt but that the Trichobasis glumarum is nothing more than the Uredo of Puccinia rubigo vera, for although the spores are not very distinctly verrucose, yet careful examination of them,

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[*] Körnicke, *Land und Forstw. Zeitg.* 1865, No. 50.
[†] Fuckel, *Symbol Mycol. Nachtr.*, ii., p. 16.

[*] Thümen, *Herbarum Mycol. Œconom.*, No. 451.

dry, will show that they are not smooth. The ordinary form of the Uredo spores also loses its roughness, to a great extent, when examined in water. The glumes which were earlier in the year affected with the Uredo, will be found later on to bear the teleutospores.

Appended are the spore measurements of Puccinia rubigo vera, expressed in micromills (*i.e.*, $\frac{1}{1000}$ millimetre):—

Uredo, 20—32 by 17—24.
Puccinia, 26—80 by 16—24.
Promycelium spores, 10— 15 long.
Paraphyses, 50—70 long.
Æcidium, 18—20.
Spermogonia, not known.

The Æcidium in Europe is known to occur on *—

Cynoglossum officinale.
Borago officinalis.
Anchusa officinalis.
Lycopsis arvensis.
Nonea pulla.
Symphytum officinale.
,, tuberosum.
Cerinthe minor.
,, alpina.
Echium vulgare.
Pulmonaria officinalis.
,, tuberosa.
Lithospermum arvense.

Puccinia rubigo vera in Europe is known to occur on *

Calamagrostis epigejos.
Holcus lanatus.
,, mollis.
Arrhenatherum elatus.
Avena flavescens.
Festuca elatior.
Bromus secalinus.
,, mollis.
,, arvensis
Bromus asper.
Triticum vulgare.
Secale cereale.
Hordeum vulgare.
,, distichum.
,, murinum.
,, secalinum.
Lolium temulentum.

Charles B. Plowright, Kings Lynn, July 24.

CHAPTER III.

CAN WHEAT MILDEW PROPAGATE ITSELF APART FROM THE BARBERRY?

If any botanist or agriculturist residing in Norfolk or in the Fen district were asked whether Wheat ever became mildewed without the presence of the Barberry he would unhesitatingly answer in the affirmative, for the simple reason that we have the Wheat mildewed to a greater or less extent every year, while the Barberry is a very rare shrub with us. This is one of the strongest arguments used by those who oppose the theory of the heterœcism of Puccinia graminis, but apart from this consideration it is of importance practically. Nothing seems more natural than to suppose the promycelium spores of Puccinia graminis should penetrate the leaf or stem of the Wheat plant through the epidermis by their germ-tubes, and so give rise to the Uredo. But De Bary† distinctly says :—"The germination of the spores formed by the promycelium gave me previously the unexpected result that the germ-tubes do not bore through the epidermis of the host plant. In various parts of Triticum repens, T. vulgaris, and Avena sativa they remained as if they had been sown upon glass. The tubes turned irregularly in the most different directions, and died off quickly ; the grass plant on which they were sown remaining intact." It is obvious that De Bary is clearly decided in his own mind that these promycelium spores do not penetrate the epidermis not only of Wheat, but also of Twitch and Oat plants. In my former paper on this subject‡ two experiments are mentioned, one of which was unsuccessful ; but in the other, performed on April 17, 1882, five Wheat plants were infected with freely germinating promycelium spores of P. graminis ; on April 24 the plants were uncovered, and on May 7 the true Uredo graminis appeared upon one plant. From the fact of these plants being exposed to accidental infection from the atmosphere from April 24 to May 7 a source of possible error is admitted, which considerably diminishes the value of this culture, for although this experiment was performed at a time of year when the spores of Uredo graminis and Æcidium berberidis were exceedingly unlikely to be blowing about in the atmosphere, yet my last year's experience in Uredine culture impressed me very strongly with the extreme care necessary to exclude error from the entrance of foreign spores. Still, it must be remembered that the control plants were growing all the time this experiment was going on in the open air in the same garden, and yet showed no traces of the fungus. This experiment was repeated later on in a more careful manner. On June 29 four flower pots were filled with earth, and had Wheat planted in them. They were at once placed under two bell-glasses. Next day some pieces of grass with abundance of last year's Puccinia graminis on them were laid upon two of the flower pots under one of the bell-glasses. The P. graminis had not at that time germinated ; it had been for some time in my study, and previously to being employed in this experiment was soaked for about a week in pure water. The pots were watered and examined from time to time, and on July 28 the Wheat growing in the pots on which the grass stems were laid had true Uredo graminis upon it. The other Wheat plants remained free from the fungus up to the end of August. The bell-glasses were thoroughly cleansed before being used, by being washed inside and out with a strong solution of cupric sulphate. The earth used was purposely taken from a few inches below the surface so as to be free from stray Uredo spores, and the flower-pots were new ones. The plants were uncovered for watering three or, at the most, four times, and then only for a few seconds. The grass on which the P. graminis was, was cut into short pieces, and laid flat upon the earth, so that as soon as the young Wheat plants appeared above the surface they came into direct contact with it. Some light will also be thrown upon this subject by the investigation of the other heterœcismal Puccinia. P. rubigo vera has this year been extremely abundant; hardly a specimen of Holchus lanatus exists in this neighbourhood without harbouring it. But the Æcidium which occurs on various Boraginaceæ I have never been able to find. This Puccinia recurs year after year on the same plants of Holchus, with no Boraginaceous plant in the vicinity. Again, only yesterday I walked over some pasture land not very long reclaimed from the sea on which Puccinia coronata in both the Uredo and Teleutospore state occurred in the greatest profusion; and to my certain knowledge there is no shrub of either Rhamnus frangula nor cathartica within 4 miles. All this points to but one conclusion, namely, that the heterœcismal Pucciniæ can propagate themselves without the intervention of their Æcidia.

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* Winter G., *Synopsis Uredineen ünd ihrer Nakrpflanzen* (reprint from *Hedwigia*), p. 12.

† De Bary, *Neue Untersuchungen uber Uredineen*, p. 24—25.

‡ Plowright, *Gardeners' Chronicle*, August 19, 1882, p. 233.

The heterœcismal Pucciniæ at present known are all found either upon grasses or carices. In this county they are seven in number, namely, P. graminis, with its Æcidium on Barberry; P. rubigo vera, with its Æcidium on Boraginaceæ; P. coronata, with its Æcidium on Rhamnus frangula and cathartica; P. Moliniæ, with its Æcidium on Orchis latifolia, &c.; P. poarum, with its Æcidium on Tussilago farfara; P. caricis, with its Æcidium on Urtica dioica; P. sylvatica, with its Æcidium on Taraxacum officinale. As the Æcidium state is known to be the product of the promycelium spores, one is led to consider whether there be anything in the structure of the grasses and carices inimical to the entrance of the germ-tubes of these spores. In the passage already quoted from De Bary he speaks of the germ-tubes of the promycelium spores not boring through the epidermis, and suggestively adds that "they remained as if they had been sown upon glass." Here I believe lies the explanation, these germ tubes do not bore through the epidermis because they cannot. The amount of silica in the Graminæ is well known, and has been spoken of as "Nature's waterproof mantle;" it may with equal truth be said to be "Nature's spore-proof mantle." The germ-tubes of the promycelium spores, it will be remembered, are very diminutive structures compared to most of the Uredo and Æcidium spores. They are not long enough to travel over the surface of the blade and search for the stomata as those of the latter spore-forms do. The last-named germ-tubes do veritably search for the stomata. The main tube almost always travels across the blade at right angles to its long axis, sending off here and there short rectangular branches when it passes over the junction of two cells, as is shown in figures in my previous paper.* Of course the minute germ-tube of the promycelium spores is quite inadequate to do this. There is no reason, however, why these germ-tubes should not enter any part of the Wheat plant that is not armour-plated. In the two experiments just mentioned, in which Wheat plants grown under glass were so placed that their plumules came in contact with the teleutospores of P. graminis as soon as they came above-ground, became infected with the fungus, while the control plant remained healthy. That this is by no means an impossible suggestion is shown by the analogous case of Cystopus candidus, in which De Bary found the plants became infected with the fungus through the entrance of the zoospore germ-tubes into the cotyledons. But we are not confined to the plumule as the only vulnerable point; the rootlets may be points of entrance. Considering how constantly stray Wheat plants growing upon manure heaps are affected with mildew, this mode of entrance does not seem at all improbable under those conditions. The roots and root-stock of the Wheat plant are more likely to be in contact with the germinating teleutospores than when the plant is grown in the ground. The fact, too, of perennial grasses being annually the hosts of various heterœcismal Pucciniæ would also seem to indicate the possibility of the plants being infected through some other channel than the plumule. These points are, however, at present only suggestions, which I hope to put to the proof next spring. *Charles B. Plowright, Kings Lynn.*

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* See p. 6, fig. 1, *o*; p. 9, fig. 3, *i*.

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